STUDIES IN SPORT, PHYSICAL EDUCATION AND HEALTH 15

CARMELO BOSCO

STRETCH-SHORTENING CYCLE IN SKELETAL MUSCLE FUNCTION

WITH SPECIAL REFERENCE TO ELASTIC ENERGY AND POTENTIATION OF MYOELECTRICAL ACTIVITY

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Mechanical behaviour of human leg extensor muscles was investigated under conditions of varied stretch-shortening (eccentric-concentric) cycle movements of the vertical jump. In these exercises the muscular performance was always greater than that in pure concentric contraction. The enhanced performance was due to the storage and re-use of elastic energy. When examined with 226 subjects this elastic potentiation was observed to be both sex and age dependent. In another series of experiments the pre-stretch movement prior to shortening shifted the force-velocity curve to the right. Similarly the net mechanical efficiency of the positive work was increased from 20 % (no rebound jumps) to 30-40 % (rebound jumps). The results also indicated that not only the mechanical behaviour of muscle was modified due to stretching of active muscle, but the electromyographic activity was also increased, but primarily during the eccentric phase of the cycle. Elastic potentiation was also sensitive to the duration and velocity of the stretch and suggestion was made that, although the influence of muscle structure was not examined directly in the present study, utilization of elastic energy may occur differently according to whether slow or fast muscles were activated under various conditions of the stretch-shortening cycle.

muscle mechanics, elastic energy, myoelectrical potentiation, muscle efficiency, stretch potentiation effect.

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PREFACE

This thesis is based on the following papers, which will be referred to by their Roman numerals:

I BOSCO, C., and P. V. KOMI. Influence of aging on the mechanical behaviour of leg extensor muscles. Eur. J. Appl. Physiol. 45: 209-219, 1980.

II BOSCO, C., and P. V. KOMI. Potentiation of mechanical behaviour of the human skeletal muscle through prestretching. Acta Physiol. Scand. 106: 467-472, 1979.

III BOSCO, C., P. V. KOMI, and A. ITO. Prestretch potentiation of human skeletal muscle during ballistic movement. Acta Physiol. Scand. 111: 135-140, 1981.

IV BOSCO, C., J. T. VIITASALO, P. V. KOMI, and P. LUHTANEN. Combined effect of elastic energy and myoelectrical potentiation during stretch-shortening cycle exercise. Acta Physiol. Scand. in press 1982.

V BOSCO, C., A. ITO, P. V. KOMI, P. LUHTANEN, P. RAHKILA, H. RUSKO, and J. T. VIITASALO. Neuromuscular function and mechanical efficiency of human leg extensor muscles during jumping exercises. Acta Physiol. Scand. in press 1982.

The studies were carried out at the Department of Biology of Physical Activity, University of Jyväskylä, Finland, during the years 1975-1981, with collaboration of several persons to whom I wish to express my sincere gratitude:

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Jyväskylä, February 1982

Carmelo Bosco

1. INTRODUCTION

In natural movements the lengths of muscles, the extent to which they are activated, and the tension they exert change continuously. The relationship between muscle length, velocity of lengthening or shortening, and the frequency of the stimulus which effects the muscle tension interact in ways that are seldom simple. The behaviour of the muscle is generally easier to understand when the whole course of a movement is controlled as in the study of animal muscle preparation. However, in normal motion the muscle seldom shortens at constant speed; further, in maximal voluntary contraction not all motor units may be active simultaneously, as occurs during stimulation of isolated muscle. To understand the mechanical behaviour of skeletal muscle, when controlled by the nervous system, from findings which arose from direct investigation of isolated muscle preparation is, therefore, rather complex. In spite of this, most of the basic knowledge, necessary for the interpretation and explanation of the function of muscle, and of its mechanical properties, has been reached by studying muscle in vitro.

To match the peculiar viscoelastic properties of the muscle, and to explain its mechanical activity, the muscle has been considered as a mechanical unit, consisting of a damped oscillator including viscoelastic elements (Levin and Wyman 1927, Hill 1938). Hill (1949) proposed a model for the skeletal muscle, which referred the mechanical properties of the muscles to three elements: an active contractile element representing the processes by which the muscle responds to stimulation, and two passive elastic elements: a series elastic element, and a parallel elastic element. The last of these is thought to reside within the sarcolemma and fasciae (e.g. endomysium, perimysium, epimysium) and is put under tension by lengthening of the muscle. It is responsible for the force measured in a relaxed muscle when it is stretched beyond its resting length. The series elastic element was thought to reside mainly in the tendons and tendon bundles within the muscle. But A.V. Hill (1950) suggested that part of the "series" compliance could reside within the contractile component itself. In this connection, Jewell and Wilkie (1958) pointed out that about half of the series compliance of frog sartorius is located in the pelvic tendon and half is distributed along the muscle fibers. Only recently, after the sliding filament theory had been developed by A.F. Huxley (1957), Huxley and Simmons (1971) were able to show that most of the elastic compliance of muscle is located within the cross-bridges between actin and myosin. Evidence that part of the elastic compliance resides within the active component of the muscle was also found by Rüegg (1971), Rack and Westbury (1974), and Flitney and Hirst (1978).

The elastic properties of the muscles have recently received increased attention, because of their great role in determining the mechanical behaviour of muscles. According to Hill (1950) the mechanical energy stored in the series elastic component can be used to produce a final velocity greater than that at which the contractile component itself can shorten. Cavagna et al. (1965) have pointed out that stretching of an activated muscle leads to greater work and power output during a subsequent shortening phase of contraction. In addition Cavagna and Citterio (1974), working on isolated frog striated muscle, have concluded that stretching of an active muscle temporarily modifies its elastic characteristics, causing the muscle to work more efficiently during the subsequent positive work phase. Thus, it seems that elastic energy is stored during the negative (eccentric) work and recovered in part during the following positive (concentric) work phase. However, this potential energy can be wasted as heat (Fenn and Marsh 1935) if the eccentric contraction is not immediately followed by the concentric one (Hill 1961, Cavagna et al. 1968). This is due to the transient character of the muscle elasticity changes, and makes a quick movement more profitable than a slow one (Cavagna and Citterio 1974).

The potentiation of muscular performance, observed after an active muscle has been stretched, and which has been attributed to the storage and utilization of elastic energy, has been investigated not only in studies of isolated muscle preparation but also in man, e.g. in jumping exercises (Marey and Demeny 1885, Cavagna et al. 1971, Asmussen and Bonde-Petersen 1974a, Asmussen et al. 1976, Komi and Bosco 1978a). It has also been observed that both net mechanical efficiency and apparent mechanical efficiency, estimated in a large variety of exercises performed with a stretch-shortening cycle pattern, have been found to be greater than that expected from a maximal efficiency of transformation of chemical energy into mechanical work. Therefore, part of the positive work measured has been assumed to be delivered, free of cost, during the recoil of the previously stretched elastic elements. It has been suggested that this occurs in walking (e.g. Cavagna and Kaneko 1977), running (e.g. Cavagna et al. 1964, 1976, Cavagna and Kaneko 1977, Ito et al. 1981), rebound experiments (e.g. Margaria et al. 1963, Thys et al. 1972, 1975, Asmussen and Bonde-Petersen 1974b) and in load running exercise (Pugh 1971, Lloyd and Zachs 1972, Zachs 1973, Asmussen and Bonde-Petersen 1974b).

In the studies with isolated muscle preparation, the nervous connections have not been intact, and therefore the increase in performance of the skeletal muscle through pre-stretch in these studies can be attributed solely to the storage and utilization of elastic energy and their influence on the contractile machinery. On the other hand, in human experiments when the nervous system is intact, part of this "potentiation of performance" through pre-stretching might as well be attributed to a reflex potentiation.

Evidence has been presented to show that fast stretch of an active muscle causes substantial stretch reflex potentiation via Ia afferent from muscle spindles (e.g. Prochazka et al. 1977, Gottlieb and Agarwal 1979). It is possible that stretching of active muscle in man also causes reflex potentiation via a cortical loop. There are indications that this reflex may reach the muscle within approximately 40 - 70 ms from the beginning of the stretch (e.g. Iles 1977, Gottlieb and Agarwal 1979, Chan et al. 1978). Thus, if a motion is performed with a large range amplitude, reflex action would effect the eccentric phase of the stretch-shortening cycle. On the other hand, if the range of movement is short and its motion fast, the myotatic reflex response might occur during the positive work phase. According to Nichols and Houk (1976) the reflex action would be enhanced by the fact that newly recruited motor units would develop more force at the stretch length than at the initial length. Therefore, it seems that the relative contributions of reflex action upon the mechanical properties of active muscle may be different. Thus, the viscoelastic properties of the muscles are not only able to match the external perturbations and disturbances (Grillner 1972), but, it seems, to operate properly in connection with that part of the nervous system, which is responsible for the internal variation of muscle force output.

The storage of elastic energy and its utilization has been investigated earlier in our laboratory (Komi and Bosco 1978a, b) utilizing the technique of Asmussen and Bonde-Petersen (1974a). This consists of performing maximal vertical jumps on a force-platform with and without previous stretch of leg extensor muscles. In a previous investigation an attempt was made to study how subjects with different fiber compositions in their m. vastus lateralis were able to utilize elastic energy. Furthermore, it was thought useful to study the possible differences in storage capacity and utilization of elastic energy between men and women of comparable physical condition. From this study, it was concluded that male subjects usually can sustain higher stretch loads than their female counterparts. On the other hand, females were able to utilize a greater proportion of the stored elastic energy. In general those findings were in good agreement with earlier results (e.g. Cavagna et al. 1971, Asmussen and Bonde-Petersen 1974a); and in addition, the testing technique employed was shown to be very satisfactory. Therefore it was logical to examine how this method is applicable to and sensitive for the differentation of performance characteristics in different age and sex groups (study I).

The problem of elasticity was studied further e.g. in connection with the mechanical behaviour of skeletal muscle. Thus it was investigated how jumps performed with a stretch-shortening cycle could modify the force-velocity (F-V) and power-velocity (P-V) relationships as compared to the basic relationship which can be obtained utilizing jumps performed without prestretch. In addition, the basic interrelationships between the various mechanical parameters of the stretch-shortening cycle were examined (studies II and III).

It is also expected that the final performance obtained after a muscle has been actively stretched depends on the pattern of neural activation of the muscle. Therefore, the concomitant influence of elasticity and nervous potentiation on muscular performance was examined (study IV).

The practical meaning of elastic potentiation was evaluated for the work economy itself. This led to the study of mechanical efficiency and its dependence on elastic potentiation (study V).

2. RESEARCH METHODS

2.1. Subjects

A total of 249 healthy subjects were studied. All the subjects were residents in the town of Jyväskylä (Middle Finland). One hundred and thirteen males and the same number of females, divided into groups according to age and sex, were classified as untrained or moderately trained (groups I-II according to Saltin and Grimby 1968) with respect to occupational and spare time physical activity (study I). The other twenty three subjects were well experienced athletes and were familiar with the test procedure (studies II, III, IV, V). Table 1 summarizes the number of subjects and the age, height and weight of each subject group.

2.2. Statistical methods

Conventional statistical methods were employed to calculate the mean ($\bar{x}$), standard deviation (SD), standard error of the mean (SE) and linear correlation coefficient (r). When useful, intra- and interindividual differences, and differences between means were tested for significance using Student's t-test. The accuracy of the methods used has been evaluated including error of measurement. The reproducibility of the measurements was conducted on duplicate analysis and expressed as a correlation coefficient.

2.3. Testing procedures and data collection

2.3.1. Jumping performances (I-V)

Each subject performed maximal voluntary vertical jumps on the force-platform (Komi et al. 1974), sensitive to the vertical

Table 1. Anthropometrical characteristics of the subjects (Mean ± SD).

Subject groups	n	Age (years)	Height (cm)	Weight (kg)
Study I				
Age group				
4- 6 ♂	10	4.6 ± 1.2	110.3 ± 6.2	18.1 ± 2.2
4- 6 ♀	11	4.9 ± 1.0	110.5 ± 9.0	18.6 ± 3.4
13-17 ♂	19	14.5 ± 1.1	170.3 ± 7.8	56.4 ± 8.7
9-12 ♀	15	10.8 ± 0.8	116.6 ± 9.8	35.3 ± 6.7
18-28 ♂	35	23.7 ± 2.2	178.2 ± 5.5	80.0 ± 10.0
18-26 ♀	41	21.7 ± 1.6	167.2 ± 5.2	58.8 ± 5.4
29-40 ♂	16	37.1 ± 3.7	176.9 ± 4.7	78.9 ± 7.4
34-40 ♀	16	26.9 ± 1.4	164.2 ± 4.7	64.4 ± 5.9
41-49 ♂	18	45.1 ± 3.2	173.8 ± 4.4	77.1 ± 12.1
41-48 ♀	15	43.4 ± 2.1	162.9 ± 4.6	68.3 ± 9.3
54-65 ♂	4	60.0 ± 4.5	168.8 ± 2.5	75.8 ± 11.9
51-64 ♀	11	61.2 ± 6.7	160.2 ± 5.2	62.2 ± 8.0
71-73 ♂	11	72.5 ± 0.5	166.2 ± 3.8	74.7 ± 7.6
71-73 ♀	14	72.3 ± 0.4	158.3 ± 4.75	66.3 ± 11.6
Study II				
Volleyball player ♂	1	27.0	187.0	84.0
Study III				
Power athletes ♂	14	22.9 ± 3.5	181.6 ± 8.2	74.1 ± 7.0
Study IV				
Power athletes ♂	3	26.0 ± 4.3	179.7 ± 5.8	73.0 ± 3.7
Study V				
Phys. educ. students ♂	5	28.8 ± 4.9	179.0 ± 6.0	77.9 ± 6.8

ground reaction force and with a natural frequency of 100 Hz, in the following different ways:

(a) From a semisquatting position with no allowance for preparatory counter-movement. This condition is called the squatting jump (SJ). Before to begin the vertical jumps, the subject's knee angle was preset at about 90^{o} (studies II, IV). In study I the subject's knee angle was fixed on the position they felt as the most comfortable ($\approx 90^{o}$). In study III the knee angular displacement ranged from 27^{o} to 105^{o} in all subjects. In study V performances were carried out starting from two different knee angle (90^{o}-135^{o}). The starting angle was obtained from electrogoniometer records of counter-movement jump conditions (studies II, III, IV), and rebound conditions (study V).

(b) With a preparatory counter-movement. In this counter-movement jump (CMJ) the subject started from the erect standing position on the force-platform, and the end of the counter-movement phase corresponded to the starting position in SJ. In SJ and CMJ conditions, several jumps were also performed with increased or decreased loads held by the leg extensor muscles. This was possible by performing the jumps with different barbell weights on the shoulders, ranging in weight from 15 to 220 percent of body weight (studies II, IV). To decrease the load of the body weight during the performances, several jumps were executed using assisting elastic ropes fixed between a belt around the waist of the subject and the ceiling of the laboratory. The lifting action of the elastic ropes on the body ranged between 49-214 N (study IV).

(c) Jumping after different stretch loads had been given to the active leg extensor muscle. This was achieved by letting the subjects drop down onto the force-platform from different heights (20-100 cm). This condition is called drop jump (DJ). In study I the children were tested only in DJs from 20-30 cm for safety reasons, because they were not able to tolerate higher stretch loads. The oldest subjects (71-73 yrs) were not tested in DJs. When all the drop jumps had been performed, the best drop jump (BDJ) was selected for each subject. BDJ refers to the highest rise of the center of gravity, which was attained from the various dropping heights. Examples of the vertical force-time curves are shown in Figure 1.

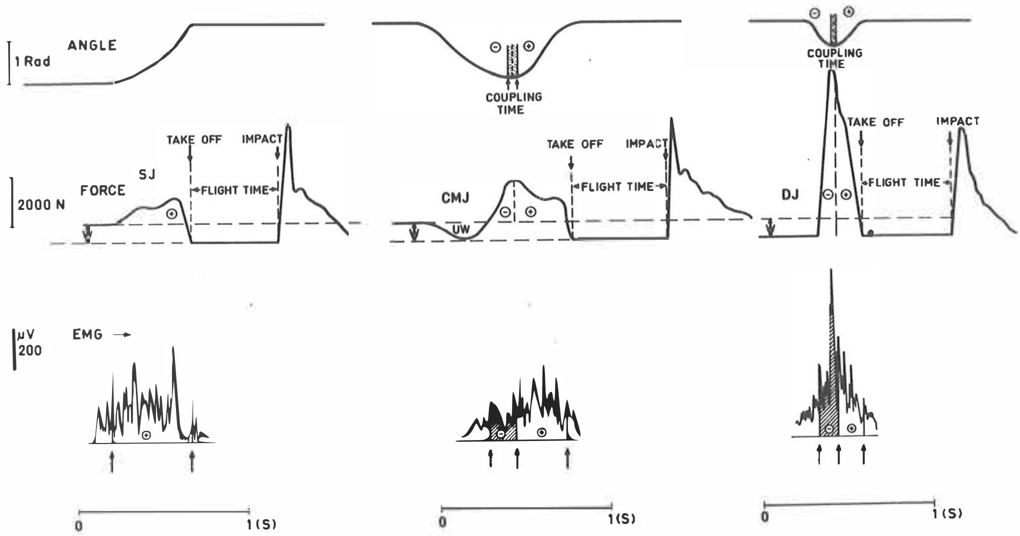

Figure 1. Example of knee angular displacement (above), vertical force-time curves (middle) and rectified EMG of m. vastus lateralis (below) in the different jumping conditions: Squatting Jump (SJ), Counter-movement Jump (CMJ) and Dropping Jump (DJ). Symbols: UW, the unweighing phase of CMJ; W, weight of the subject; ⊖, deceleration phase in eccentric (negative) work; ⊕, concentric (positive) work phase; t_{air}, the phase when the subject is in the air. The coupling time in the angular displacement record indicates the transition period between eccentric and concentric phases. The dashed line in the lower part of the figure indicates the maximal level of rectified EMG activity for SJ condition.

The total body vertical jump is a multi-joint movement, which is some function of the combined impulses of all muscles participating in the movement. Therefore, to ensure that the test jumps were performed primarily by the leg extensor muscles, the subjects were instructed to keep their hands on their hips throughout the entire jump and to minimize the lateral and horizontal displacement during the performance. The subjects were also instructed to land and take-off on the force-platform in the same position and place. Thus it was reasonable to assume that the ground reaction force time curve was proportional to the quadriceps muscle group forces. This assumption is supported by the work of Luhtanen and Komi (1978), who demonstrated that even if the trunk extension, head swing and arm swing were freely used during vertical jump performance, the contribution of the leg extensors was more than half of the total vertical force production (56 %).

2.3.2. Rhythmical vertical jumps (V)

The subjects performed rhythmical vertical jumps on the force-platform of a frequency and height chosen by each subject so that the performance could be carried out for a period of one minute. The jumps were performed in five separate one-minute series, and four of them were performed under rebound conditions. This means that the extension movement (concentric phase) took place immediately after the stretching phase (eccentric phase). The first and the second series were performed with small knee angle amplitudes (42-58 and 46-63 degrees, respectively). The third and the fourth series were performed with large knee angle amplitudes (77-105 and 91-108 degrees, respectively).

The first and the third series were carried out without, and the second and the fourth series with an additional barbell load of 20 kg on the shoulders. The fifth series was performed with no rebound condition, so that the subjects maintained a one-second isometric squatting period between the eccentric and concentric phases. Each series of jumps was also filmed using the Sanyo VTC 7100 video cassette system including a camera VC 500 and the timer (± 0.01 s) of Magnasonic VTF 100. In playback the film could be stopped at any frame.

2.3.3. Maximal isometric force (II, IV)

Maximal isometric force with zero angular velocity at all joints was also measured on the force-platform. In this test the subject was in the same position as when starting the SJ (90^{o}). The bar on the shoulders was fixed at both ends, thus allowing no movement in the joints.

2.3.4. Recording of angular displacement (II, III, IV, V)

Movement amplitude of the knee joint during each jumping performance was recorded with an electrogoniometer (Elgon) attached to the lateral side of the subject's knee joint. Elgon was also used to obtain the maximum speed of knee extension. In this test the subject lay in a supine position with the knee flexed to a starting position of 90^{o}, while both the hips and the heels were kept on the ground.

2.3.5. Electromyographic (EMG) recordings (IV, V)

Bipolar surface EMG recording (Beckman miniature-size skin electrodes) was performed from mm. vastus lateralis, vastus medialis, rectus femoris and gastrocnemius. The electrodes were fixed on to the middle part of the muscle bellies and they were kept in these constant positions during the whole course of the experiment. After amplification with Brookdeal 9432 preamplifiers (60 dB, 1 Hz - 1 kHz) these EMGs were stored simultaneously with the force and angle signals in analog form on magnetic tape (Racal Store 7). EMG was integrated for each muscle separately using the HP 21-MX computer system. Integrated EMG (IEMG) was expressed for one second period. The sampling frequency in the analog to digital conversion was 1 kHz. In study IV the number of turning points were calculated from the rectified EMG records and that value was used as a measure of quantity of EMG activity.

The sampling time for EMG was extended to the whole period of the eccentric and concentric phases of each jump separately as shown in Figure 1. The length of this period was much higher (100-500 ms) than the minimum sampling time (50 ms) suggested by Norman et al. (1978). In study V the first five and the last five jumps were averaged for each subject and for each of the four rebound series of jumps. In addition, to compare the myoelectrical activity of the selected muscles during the stretch-shortening cycle with exercises involving similar mechanical conditions but performed solely by the contractile machinery of the muscles, a series of vertical jumps (SJ) performed from different starting position (see 2.3.1.) were also monitored. In study IV similar EMG recording techniques were utilized. However, m. gastrocnemius was not monitored; and m. rectus femoris was found to behave differently from vasti muscles during the eccentric phase in CMJ and DJ (see discussion paper IV). Therefore, only the vasti muscles were averaged because of the great similarity in their activity patterns, and for each jumping condition the value of three trails were averaged.

Assuming that the quadriceps femoris was the greatest contributor to the vertical jump performances, and because the EMG electrodes were not removed between the series of jumps, IEMG values were considered comparable within subjects. Therefore, in studies IV and V the absolute value of the IEMG is presented, and related to the average force calculated for the eccentric phase (CMJ, DJ and rebound jumps) and for the concentric work (SJ, CMJ, DJ and rebound jumps). The reproducibility of IEMG and IEMG/average force estimated from analysis of duplicate measurements for different jump conditions showed to have satisfactory high values ($r = .94$, $r = .97$, respectively, $n = 6$).

2.3.6. Oxygen uptake (V)

The oxygen uptake ($\dot{V}O_2$) was recorded for a ten minutes' rest period in sitting position to measure the basal metabolic cost. $\dot{V}O_2$ during each jumping series and during the following 10 minutes recovery period in sitting position was also recorded to calculate the energetic cost of the exercise performed. A semi-automated system was used to measure lung ventilation and O_2- and CO_2-concentrations in the expired air (Rusko et al. 1980) for every 1 min time period. The net oxygen cost of each jumping series (net $\dot{V}O_2$) was calculated by adding the oxygen uptake during the 1 min jumping exercise to that of the ten minutes' recovery period. The resting oxygen consumption was substracted from this eleven minutes' period. The respiratory exchange ratios during the jumping exercises were >1.0. Therefore according to this the energetic equivalent of 20.93 for O_2 was chosen.

2.3.7. Blood analysis (V)

Blood samples from the fingertip were drawn to determine lactate concentration (Biochemica Boehringer) before, 0.5 minutes and 2.5 minutes after each jumping period.

2.4. Mechanical calculation and formulas

2.4.1. Force-platform and data processing (I-V)

The vertical ground-reaction force developed during the jump performance, as recorded by the force-platform (Figure 1), and the flight time (t_{air}) gave the basis for the calculation of the following mechanical parameters: vertical velocity at take-off (V_v), height of rise of center of gravity (h), net impulse (NI), average force ($\bar{F}$), instantaneous force developed at end of the eccentric work (F_i), and average mechanical power ($\bar{\dot{W}}$).

The vertical velocity at take-off was obtained from the formula:

$$V_V = 1/2 \times t_{air} \times g \qquad (1)$$

in which g = acceleration due to gravity ($9.81\ m/s^2$).

The height of rise (h) of the center of gravity over that obtaining at take-off can then be computed

$$h = \frac{V_V^2}{2 \times g} \qquad (2)$$

The final vertical velocity at take-off was also computed by integration of the acceleration from the force-time curve. The value of this computation was similar (± 0.001 m/s) to the V_V calculated from formula (1).

Net impulse was obtained as follows:

$$NI = \int (F(t)-W)\ dt = m \times V_V \qquad (3)$$

where F = force, W = weight of the subject, m = mass, V_V = vertical velocity at take-off.

Average force ($\bar{F}$) was computed using the following formula:

$$\bar{F} = \frac{m \times V_V}{t} \qquad (4)$$

Here t is the time of contact with the platform during the work performance.

Vertical acceleration, velocity and displacement were calculated through integration from force-time curve on the Hewlett-Packard Model 9810 A desk computer. The average mechanical power ($\bar{W}$) was then computed through the change of mechanical energy (translatory and potential), which was assumed to represent the total mechanical work (W). To calculate mechanical power for both eccentric and concentric phases the total work was divided for the respective contact time.

In study IV the net force of leg extensors was calculated subtracting the elastic force of the ropes from the total force. In calculations of mechanical work and power, the role of the elastic ropes was separated.

In DJ condition a positive value for ground reaction force is obtained at the moment of touchdown on the force-platform, although the work is negative (eccentric phase), as denoted in Figure 1. In order to estimate the periods of negative and positive phases from the total contact period, the negative contact time was first calculated by using the formula of Asmussen and Bonde-Petersen (1974a) as follows:

Negative contact time

$$(t_{neg}) = \frac{V_v \times t_{tot}}{V_v + V_d} \tag{5}$$

in which V_v = vertical take-off velocity, t_{tot} = total contact time, V_d = downward vertical velocity.

V_d can be obtained from the formula:

$$V_d = \sqrt{2gh} \tag{6}$$

in which h = dropping height, g = acceleration of gravity (9.81 m/s^2).

To calculate the average force during the eccentric work in CMJ and DJ, the formula (4) was employed, where V_v was substituted by the downward vertical velocity, which was computed by integration of the acceleration from the force-time curve in CMJ and by the formula (6) for DJ.

2.4.2. Elgon data processing (II, III, IV, V)

Angular displacement of the knee joint was recorded with Elgon which was calibrated to read zero when the subject was standing erect. In jumping performance where the stretch-shortening cycle occured, both negative and positive phases could be computed for the knee joint (Figure 1). The transition period which links the negative phase with the positive phase was called "coupling time". This period is represented by the shaded area of Figure 1, and shows the position of the Elgon record where the knee angle stays the same, and supposedly no change of length occurs in the knee extensor muscles. The length of this phase was measured manually using the tangent of the knee angular displacement curves. The accuracy of these measurements were ± 2 ms and ± 3 ms, respectively, for small and large-amplitude jumps.

2.4.3. Mechanical efficiency (V)

The mechanical efficiency of positive work was assumed to be represented by the ratio of mechanical work performed during the positive phase (W_{pos}) and the respective energetic cost (E_{pos}) calculated from formula (8). The total mechanical work performed by the subjects was calculated from video film analysis through change of potential energy using the formula:

$$W = \sum_{i=1}^{n} |\Delta mgh_i| \qquad (7)$$

where W = total mechanical work in one minute, n = number of jumps in one minute, m = mass of subject with or without extra load, $g = 9.81\ m/s^2$ and h_i = change in the height of the center of gravity (C.G.) between the highest and lowest point in jump i (estimated from the movements of the head, which was assumed to reflect the parallel changes in C.G.).

A difference of ± 3.7 % was found between the displacement of the head and the displacement of the C. of G. calculated by integration of the acceleration from the force-time curve recorded from the force-platform.

The work from the lowest point during contact to the highest point during flight time was assumed to be positive (W_{pos}). The negative work (W_{neg}) was assumed to be numerically equal to W_{pos} and to have the energetic efficiency of -1.2 (e.g. Margaria 1938, 1968, Asmussen 1952, Davies and Barnes 1972). Therefore the energetic cost of positive work (E_{pos}) was calculated according to the following formula:

$$E_{pos}\ (\mathrm{kJ}) = \mathrm{Net}\ \dot{V}_{O_2} \times 20.93 - \frac{W_{neg}}{1.2} \qquad (8)$$

where 20.93 is the energetic equivalent of $\dot{V}_{O_2}$ ($1 \times \mathrm{min}^{-1}$) into $\mathrm{kJ} \times \mathrm{min}^{-1}$.

3. RESULTS

The findings presented below represent the most significant conclusions which can be drawn from the total information gathered. For more details the original work should be consulted.

3.1. Prestretch potentiation related to age (I)

The results of the present study clearly demonstrated that male subjects had much better performance than the female subjects (Table 2, study I). In both SJ and CMJ the peak performance in the height of rise of center of gravity occured at a younger age in females (9-12 yrs) than in males (18-28 yrs) (Figures 2 and 3, study I). These performances were for females about 30 % lower, in both SJ and CMJ conditions, than for their male counterparts. However, in the other mechanical parameters both male and female groups reached peak values in the 20-30 years age group; and thereafter a nearly linear decrease in performance was observed as the age increased. Assuming that the performance difference between CMJ and SJ gives reliable information about the effect caused by previous stretching of the muscle, we can observe that this potentiation effect was not very marked in children (Figure 2) and accounted for about 50 % of the maximal reached at the age of 20-30 yrs; after which an almost linear decrease with age was noted, until at the age 60-70 yrs only 30-35 % of the maximal was reached.

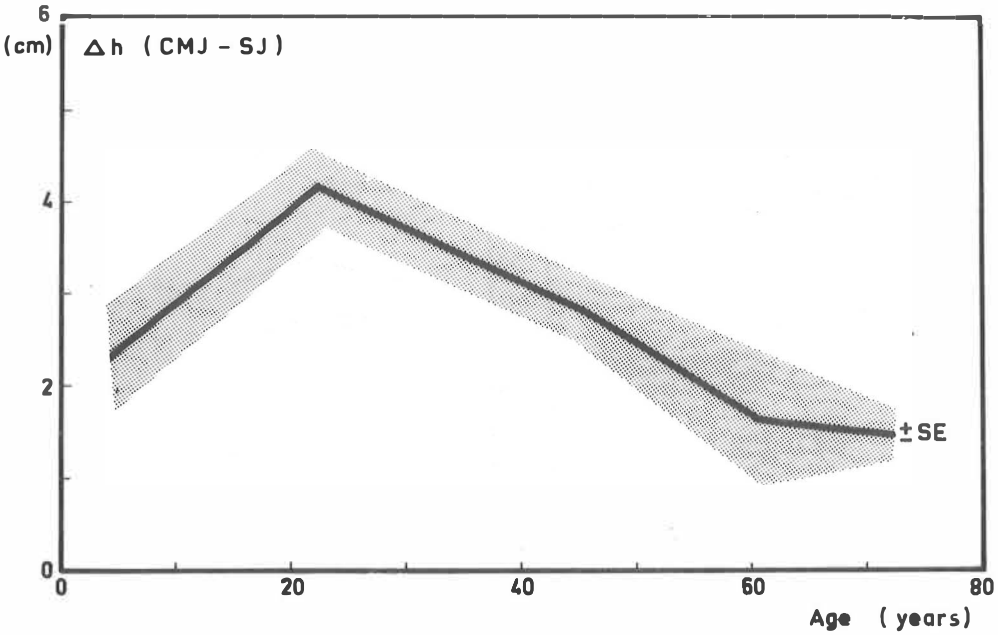

Figure 2. Performance differences between counter-movement jump and squatting jump for all the age groups studied. Values are means ± SE.

3.2. Effect of dropping height on the aging process (I)

The variation of stretch potentiation with age can also be studied by changing the magnitude of stretching loads. This was obtained by asking the subjects to execute a vertical jump immediately after dropping from different heights (20-100 cm). In Figure 3 it is shown that the "breaking points", indicating the maximum tolerance of stretch load, increased up to the age of 20-25 years and then decreased. Both children (4-6 yrs) and the oldest age group tested (50-60 yrs) were not able to reach higher value than 50 % of the maximal noted at age of 20-25 yrs.

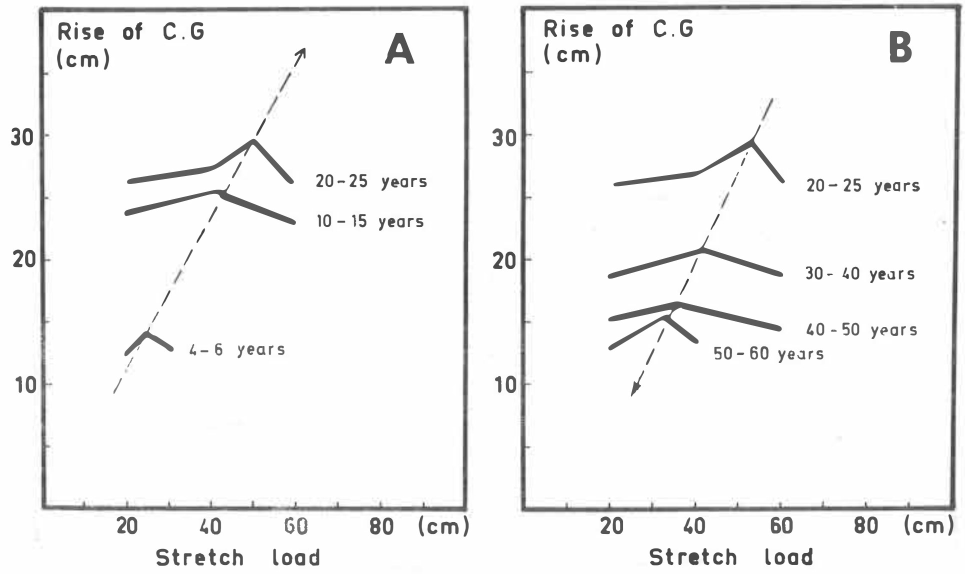

Figure 3. A&B. Variation of the rise of center of gravity of jump performance in relation to the dropping height. Each age group represents the mean value of both sexes.

3.3. Effect of prestretch on force-velocity relationship (II)

The enhancement of the total mechanical performance after stretching of leg extensor muscle, in jumping exercise, can also be demonstrated by increasing the subject's body weight. In this part of the study, when the force-velocity (F-V) relationship of concentric work was examined in both SJ and CMJ conditions, a substantial displacement of F-V curve to the right was observed in CMJ (Figure 3, study II). For example, in conditions where no extra load was used on the shoulders, the force in squatting jump (knee angular velocity 4.5 rad x s^{-1}) was 603 N. In counter-movement jump the corresponding value was 879, performed with the knee angular velocity of 7.0 rad x s^{-1}.

This change in force indicated an average potentiation of 46 %. When the analysis was extended to the power-velocity (P-V) relationship between squatting jump and dropping jump conditions, the magnitude of potentiation effects observed in DJ was much greater (100-450 %) than that noted in CMJ condition (Figure 4, study II).

3.4. Mechanical parameters and stretch potentiation (III)

The role of external loads (e.g. gravitational pull) in stretch-shortening exercise seems to be of primary importance in regulating the mechanical behaviour of the muscle. This can be represented by e.g. movement amplitude, stretching speed, average force during eccentric work, force reached at end of the stretch, and coupling time. Some of these mechanical parameters were closely intercorrelated (Table 2). For example, the coupling time was longer, the larger the movement amplitude ($r = .46$; $p < .001$). In addition, correlation analysis revealed that several mechanical parameters were correlated with the "potentiation" variable expressed as average force difference ($\Delta\bar{F}$) and average power difference ($\Delta\bar{W}$) between CMJ and SJ. The value of $\Delta\bar{F}$ was correlated, for example, positively with prestretching speed ($r = .53$; $p < .001$), negatively with coupling time ($r = -.35$; $p < .01$) and positively with instantaneous force at the end of the stretch ($r = .51$; $p < .001$).

3.5. The concomitant influence of elastic energy and nervous activation in potentiating work performance (IV)

As was stated in the introduction, nervous activation was expected to interfere with elastic potentiation. In Figures 4 and 5, below, the effect of stretch on force-velocity relationship and force-power curves are presented. The mechanical behaviour of leg extensor muscle of the subjects studied was, under all

Table 2. Correlation matrix for the various parameters calculated from the force-time curve and Elgon records of 59 observations.

		1	2	3	4	5	6	7	8
Knee angle amplitude (α)	1								
Prestretch range (α_{ps})	2	39							
Prestretch speed (P_{ss})	3	57	17						
Prestretch time (T_{ps})	4	75	50	-68					
Coupling time (T_c)	5	46	29	-21	52				
Force at end of stretch $(-F_i)$	6	-67	-35	61	-74	-47			
Average prestretch force $(-\bar{F})$	7	-53	-47	49	-76	-47	76		
Potentiation of average force $(\Delta\bar{F})$	8	-61	-13	53	-62	-35	51	43	
Potentiation of average power $(\Delta\bar{W})$	9	-47	-23	33	-54	-41	48	37	81

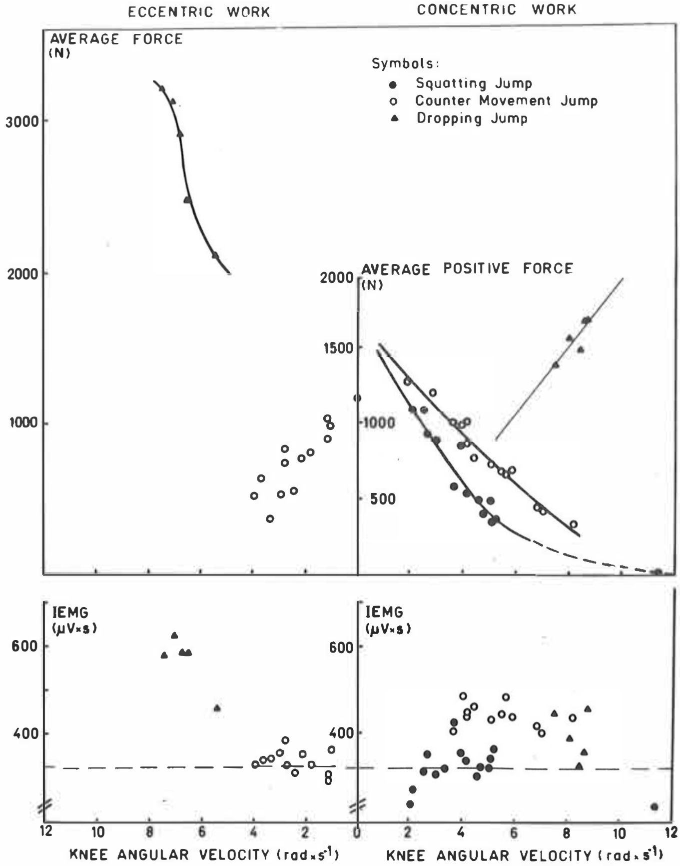

Figure 4. Average force (above) and integrated electromyography (IEMG) (below) at different knee angular velocities during eccentric (left) and concentric (right) phases for the subject A.I. measured in three different jumping conditions.

the conditions investigated, similar to that observed in study II. However, slight differences were observed among the three subjects studied, in the IEMG activities of the vasti muscles. In CMJ, for example, the subject A.I. (Figure 4) had an enhancement of IEMG activity as compared to SJ ($p < .001$). On the other hand, in the other two subjects no difference was noted (Figure 5). Differences among the three subjects studied were also

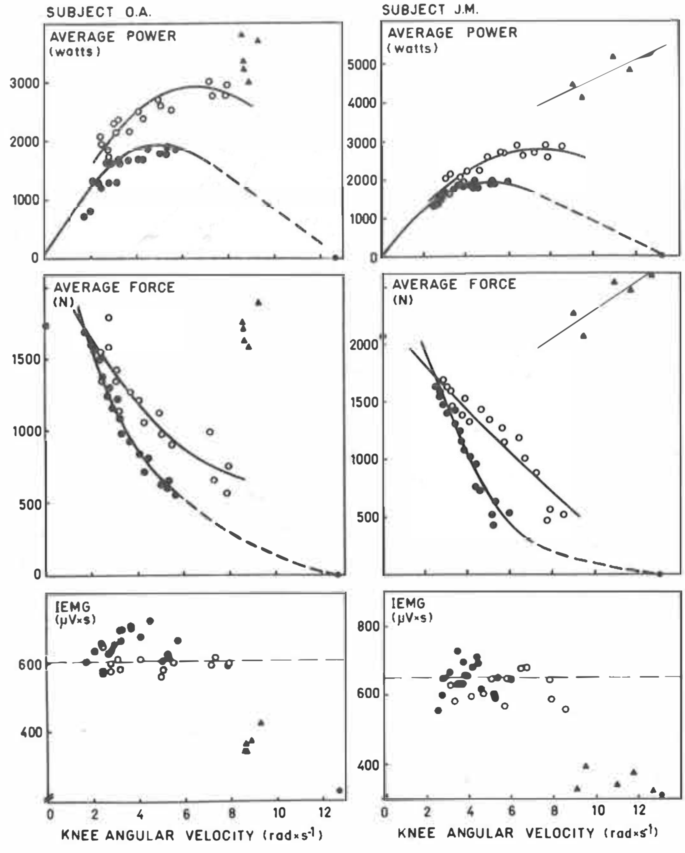

Figure 5. Power-velocity, force-velocity and IEMG-velocity curves for subjects O.A. and J.M. The curves were plotted for the concentric work and measured in the three jumping conditions of the study. For symbols see Figure 4.

observed in IEMG activity during the positive work phase in dropping jump conditions. For the subject A.I. this IEMG activity was, on the average, slight but not significantly higher than in SJ; while for the other two subjects it was much lower ($p < .001$) than in squatting jump.

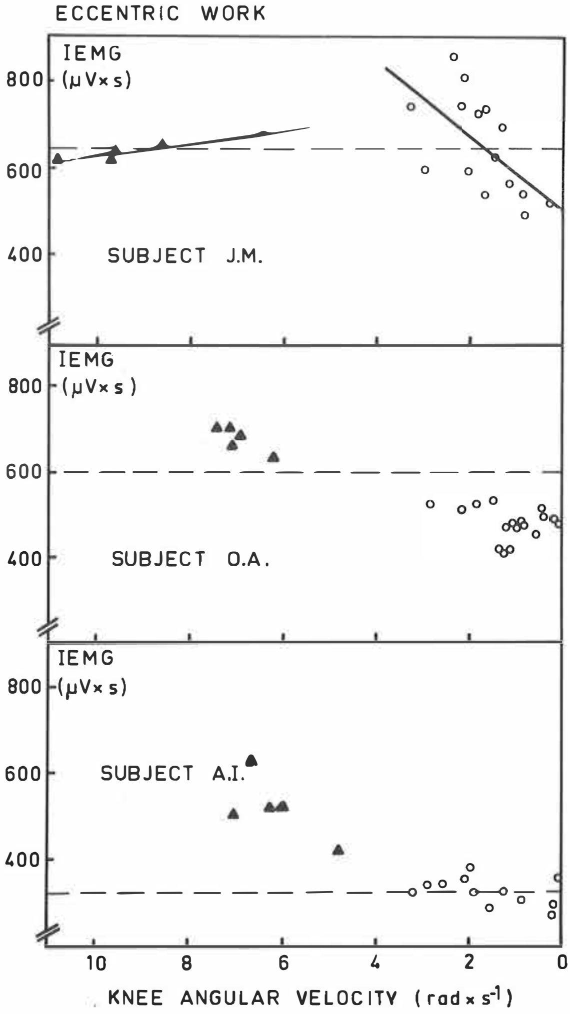

Figure 6. Integrated electromyography (IEMG) of the three subjects as a function of the knee angular velocity during eccentric work of drop jumps (▲) and countermovement jumps (●).

The comparison of IEMG activity in the eccentric phases of DJ and CMJ are presented for all subjects in Figure 6. As this figure shows, IEMG activity in the drop jump condition was much higher in subjects A.I. and O.A. than it was in any other conditions analyzed. When the drop jumps and counter-movement jumps were treated together in these subjects, IEMG increased linearly with the stretching speed. In subject J.M., the separation of the IEMG activity for counter-movement and drop jumps demonstrated, for CMJ and DJ, respectively, linear increase and decrease of IEMG activity with stretching speed.

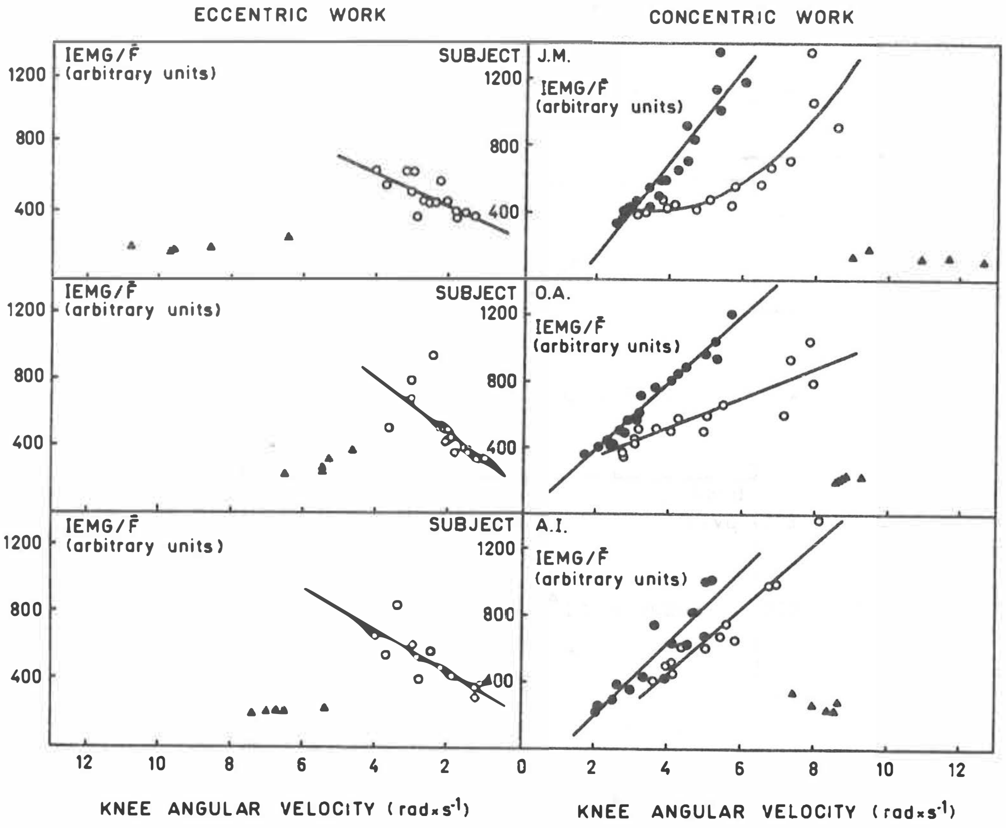

Figure 7. IEMG expressed per average force (IEMG/$\bar{F}$) at different knee angular velocities in eccentric and concentric work. For symbols and conditions see Figure 4.

In Figure 7 the IEMG activity is related to the average force of the positive and negative work phases of the jumping conditions examined. In the concentric phase, the IEMG/force ratio was always highest in the squatting jump and lowest in drop jumps. The differences between the slopes of these regression lines were also significant ($p < .001$) in all cases. In the eccentric phase, the IEMG/force ratio increased with stretching speed in counter-movement jumps, but was constant in drop jumps.

3.6. The contribution of elastic energy and nervous activation to the mechanical efficiency of human skeletal muscle (V)

The elastic potentiation shown was, as expected, observed to have a substantial influence on the mechanical efficiency of the positive work phase. Table 3 shows the net mechanical efficiency of the four series of jumps performed in rebound conditions, and the values for selected mechanical parameters. For example, the highest efficiency of W_{pos} was observed in small amplitude jumps performed without extra load 38.7 ± 5.3 %; this was associated with short coupling time (16 ± 3 ms), higher average eccentric force, and instantaneous force developed at the end of the negative work (these last were 1086 ± 392 N and 2628 ± 755 N, respectively). In contrast to this, the rebound jumps performed with large knee amplitude and without load were characterized by a lower mechanical efficiency of 30.1 ± 4.8 %, which was associated with the longer coupling time of 53 ± 9 ms, a lower average eccentric force 432 ± 103 N, and instantaneous force developed at end of the eccentric work 697 ± 200 N. The electromyographic activity monitored from selected leg extensor muscles estimated for respective negative and positive work phase in both small and large amplitude rebound jumps performed without load, is shown in Figure 8. When the ratio concentric/eccentric for IEMG is calculated, a great difference is seen between small and large amplitude jumps, showing values of 0.31 and 1.27, respectively. However, it should be emphasized that IEMG activity

Table 3. Mean (± SD) of selected mechanical parameters investigated in the first four series of jumps.

Jumping conditions (knee angle amplitude)	Net efficiency of positive work (%)	Coupling time (ms)	$\bar{F}_{ecc}$ (N)	$\bar{F}_{conc}$ (N)	F_i (N)	Angular displacement (degrees)	Stretching speed (rad x s^{-1})	Knee angular velocity during positive work (rad x s^{-1})
Small no load	38.7 ± 5.3	16 ± 3	1086 ± 392	1004 ± 228	2628 ± 755	49.3 ± 4.0	4.8 ± 0.6	6.58 ± 0.51
Small + load	38.5 ± 4.6	23 ± 10	1009 ± 412	964 ± 374	2592 ± 838	51.9 ± 6.1	4.5 ± 0.6	5.93 ± 0.76
Large no load	30.1 ± 4.8	53 ± 9	432 ± 103	421 ± 142	697 ± 200	99.3 ± 11.8	4.4 ± 0.4	5.01 ± 0.63
Large + load	26.3 ± 5.6	116 ± 53	345 ± 16	368 ± 84	552 ± 201	98.8 ± 5.4	3.6 ± 0.3	4.51 ± 0.75

during either the negative or the positive phase in the rebound jumps was always lower than that observed in a single squatting jump, in spite of the fact that the mechanical work performed was almost the same (± 4 %).

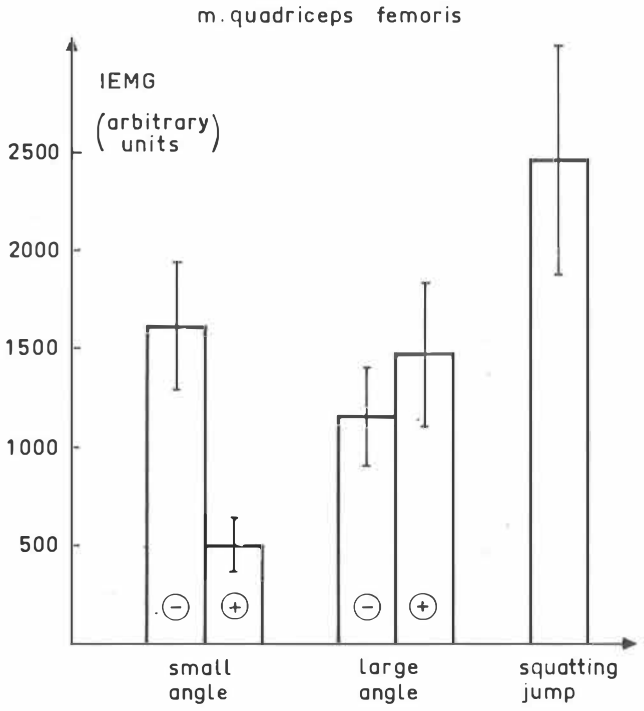

Figure 8. Integral EMG (arbitrary units) recorded from m. quadriceps femoris for negative and positive phases of small and large knee angular displacement rebound jumps performed without extra load; and for squatting jump (mean ± SD).

4. DISCUSSION

The stretching of an activated muscle modifies its internal state, and the resulting force output in subsequent positive work may be enhanced. This phenomenon was observed to occur in the present study, in accordance with expectations; the results being in line with those of previous studies (e.g. Cavagna et al. 1971, Asmussen and Bonde-Petersen 1974a, b, Komi and Bosco 1978a, b). The phenomenon was also observed when the performance variables (e.g. rise of the center of gravity (C.G.)) of CMJ and SJ were compared (Figure 2). The figure shows how this performance difference changes with age; it will be noted that the highest potentiation was reached at 20-25 years. Thereafter an almost linear decrease was observed as aging progressed.

The enhancement of performance which occurs with stretching can be attributed to a combination of utilization of elastic energy, and stretch reflex potentiation. In this investigation (study I) the exact roles of the two mechanisms were not separated experimentally, because electromyography was not performed. However, it is worth noting that the effect of potentiation on muscular behaviour showed the same biological variation with age, as maximal muscular performance (for details see study I, Figure 2), which, it has been suggested, begins between the ages of twenty to thirty years (Asmussen 1962). Thus, the present findings revealed that this enhancement in performance was related to the tension developed by the contractile machinery of the muscle during shortening contraction. This may suggest that the major contributor to the observed enhancement of performance might be of elastic nature, since the elastic compliance of muscle has been shown to be located within the cross-bridges (e.g. Huxley and Simmons 1971, Rack and Westbury 1974).

Nevertheless, it must be pointed out that the magnitude of potentiation depends on the ability of the subjects to execute optimal CMJ performances. In this particular jumping condition, a high level of coordination, and considerable ability in motor control are needed, because it is a multijoint movement, a function of the combined impulses of muscles participating in the movement through the stretch-shortening cycle. Therefore, the low potentiation observed in old subjects might also reflect an altered neuromuscular control system, which comes into being as aging progresses (Gutmann and Hanzlikova 1972). When the ability to tolerate high stretch loads was investigated in relation to the age of the subjects, similar changes were noted as those observed in SJ and CMJ. The tolerance to progressive dropping height increases from childhood up to the age of 20-25 years, and thereafter it decreases (Figure 3). The reason for this is probably that the forces developed during the eccentric work in DJ were so great that they might endanger the subjects, who consequently did not exert themselves maximally. Whether the breaking points were due to a conscious or to reflex inhibition could not be decided. It is, however, relevant to note that children were not able to tolerate even moderate stretch loads, although they were able to develop relatively high mechanical power from the SJ condition (for details see study II, Figure 2). These results support the findings of Komi et al. (1973) that in eccentric work children were unable to achieve similar values as related to their maximal isometric force as were adults. In fact, in some cases the maximal eccentric force was less than the maximal isometric force. However, the present findings might be explained by the fact that the central nervous system (CNS) at that age is not yet mature; and the threshold for Golgi tendon organs (GTO) activation is low. Thus, the proprioceptive feedback mechanism may be assumed to operate powerfully in order to protect the body against high stretch loads, especially at that age, when the muscles and particularly the bones have not yet reached maturity, and when ossification processes continue during puberty.

The decreased capacity of old subjects to stand high stretch loads might be explained as being due to the typical changes in skeletal muscle which occur with age, involving loss of muscle mass (Tzankoff and Norris 1977) and an increase of fat and connective tissue (Bakermann 1969, Gutmann 1977). This means that as age progresses there is a considerable decrease of force, since it is well established that muscle strength depends on size or transectional area of muscle, regardless of sex or training status (Ikai and Fukunaga 1968).

It has been shown that GTO is a sensitive tension receptor, particularly in response to a discrete number of motor units whose muscle fibers directly insert into tendon organs (Houk and Henneman 1967, Houk and Simon 1967, Stuart et al. 1972, Reiking et al. 1975, Jami and Petit 1976a, b, Binder et al. 1977). This means that GTOs are perhaps more sensitive to active contraction than to the passive stretching of muscle. In that case it would be reasonable to assume that, as age progresses and both force and muscular activity decrease, GTOs might adapt their firing threshold and sensibility to a lower level of tension. Thus, the neuromuscular behaviour of old subjects in response to high stretch loads could reflect such a functional adaptation. However, it should be remembered that a change with age in GTO sensibility might reflect the typical effect of senility "per se", as an impairment of biological functions.

It has already been suggested that, in addition to the utilization of the elastic energy in the muscle, the enhancement of performance in exercise involving the stretch-shortening cycle might also be due to a simultaneous increase in myoelectrical activity. The combined effect of the two mechanisms seems to operate effectively during stretch-shortening activity. Examining the force-velocity curves from performance which utilized the stretch-shortening (CMJ and DJ) it is evident that they shifted to the right when compared to those which relied only on the shortening-type contraction (squatting jump) (Figures 4 and 5). However, it is pertinent to note that both elastic energy and myoelectrical potentiation may operate differently with different individuals. For example, the performance potentiation in the positive phase of CMJ in subject A.I. can be attributed mainly to an increase of IEMG activity (Figure 4). In this case, there was an increase in motor unit activation in CMJ as compared to SJ. Subjects O.A. and J.M., on the other hand, showed no difference in IEMG activity between SJ and CMJ (Figure 5). Therefore in their cases, the increased performance in the positive phase of CMJ can be explained primarily through the effective release of the elastic energy stored in the muscle during the eccentric phase of the stretch-shortening cycle. The basic mechanism underlying this concept was introduced by Cavagna et al. (1965) and has subsequently been invoked to interpret the results of a number of studies, both of isolated muscle preparation and of intact human muscle (e.g. Cavagna et al. 1968, Asmussen and Bonde-Petersen 1974a, Komi and Bosco 1978a). At the present stage of these studies in progress, it is not possible to explain the difference of neuromuscular behaviour among individuals which has been observed.

In this connection, it is of interest to note that for the subjects O.A. and J.M. in the study, the force-velocity curves of SJ and CMJ come closer together at the low velocities and the highest force. The low difference noted between CMJ and SJ may reflect the modest contribution of elasticity in potentiating the performance of the positive work phase in CMJ. This may be due to the fact that CMJ, performed with heavy loads, was characterized by a very long stretching phase ($\gtrsim$ 500 ms). This in turn, as demonstrated in Table 2, is associated with a long coupling time, reflecting the transient period between eccentric and concentric work. If this phase is too long the stored elastic energy is lost (e.g. Cavagna et al. 1968). On the other hand, when low or no loads were used, the stretching phase was reduced in time, and the coupling time became shorter. A short coupling time is associated with high reutilization of elastic energy (see Table 2).

However, when the force-velocity curves for SJ and CMJ for the subjects A.I. are examined (Figure 4), it can be seen that at the low velocities they are not so close together as was the case for the other two subjects. This means that the decrease of potentiation in CMJ here was of modest magnitude when compared to the higher velocity side of the curves. If the enhancement of performance in CMJ relied mainly on the use of elastic energy, the deleterious influence of long coupling time might be expected to have been much more noticeable. Therefore, this observation also supports the suggestion that the enhancement of performance in CMJ for the subject A.I. can be attributed more to a potentiation of myoelectrical activity than to release of elastic energy. On the other hand, when the positive work produced under DJ conditions is examined, the substantial enhancement of the performance seems to originate mainly from the effect of the stretching. Therefore, it is relevant to point out that the negative phase of DJ was characterized by very high force, which increased when the dropping height was increased. This was correlated to an increase in average stretch (eccentric) velocity. Electromyographic activity was also very high, substantially greater than the maximum IEMG recorded from the SJ conditions. High motor unit activation with a simultaneous increase in force of the eccentric contraction increases the stiffness of the muscle (e.g. Matthews 1959, Houk et al. 1970, Rosenthal et al. 1970, Roberts et al. 1971, Nichols 1973, Nichols and Houk 1973) and thus should favor the conditions for good potentiation of muscular performance in the subsequent concentric phase. An excessive increase in the dropping heights may, however, mean that the potentiation of the force reaches a breaking point at a certain stretch load (Figure 9). This is a similar observation as the one made earlier (see Figure 3 in Komi and Bosco 1978a). Plotting of the potentiation of IEMG activity in the same graph (Figure 9) may suggest that inhibitory reflexes via e.g. Golgi tendon organs surpass the facilitatory "potentiating" effects of cortical or muscle spindle origin. This finding supports the hypothesis of Newsom (1970), that GTO has a functional role in regulating the stretch reflex. This seems to be a very fascinating aspect of the physiological properties of GTO; because besides informing the CNS concerning the recruitment of motor units over a wide range of tension (Gregory and Proske 1979), it is reasonable to assume that GTO cooperates with other proprioceptor mechanisms (e.g. the stretch reflex) to regulate muscle stiffness as well. Therefore, GTO might play an interesting role in the working economy of the muscle as well as in its mechanical behaviour. If these assumptions are correct, the present findings might suggest some practical implication, e.g. training purpose. In this connection it has been hypothesized that training with high stretch loads may increase the threshold of firing for GTO. This would then increase the possibility of storing a great amount of elastic energy into the muscle without interference from inhibitory influence of GTO (Komi and Bosco 1978b, Bosco et al. 1979). At this point one might argue whether these findings can be generalized as a biological phenomenon or if the limited number of the subjects might restrict the interpretation of the results. However, although

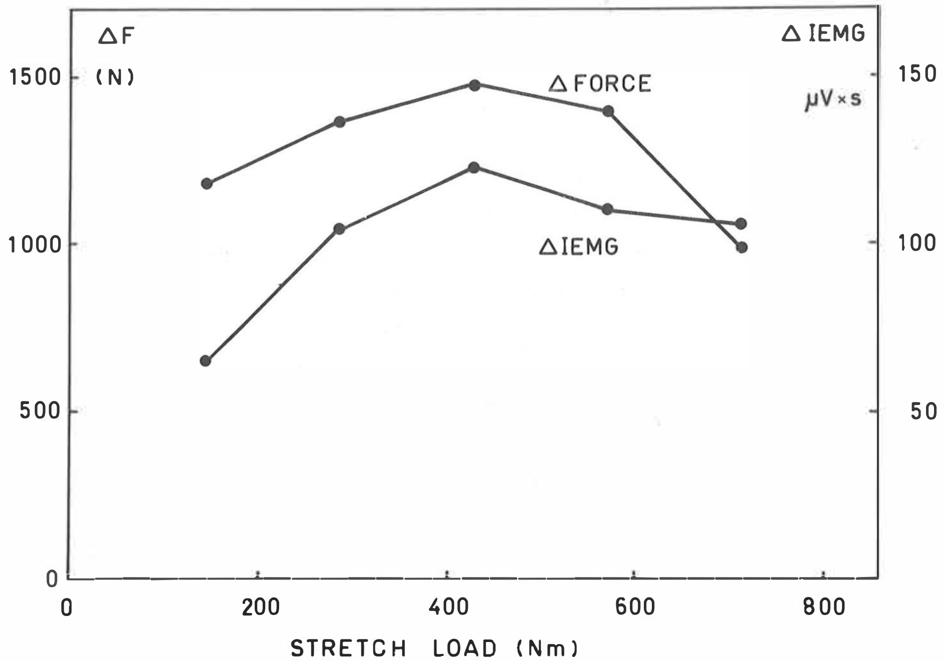

Figure 9. The differences in average force (ΔF) and integrated EMG (ΔIEMG) between the concentric phase of the drop jumps and squatting jumps, measured at different drop jumps stretch loads.

the present observations could be considered with these limitations in mind, it is relevant to point out that further studies (Bosco and Viitasalo 1982, Viitasalo and Bosco 1982), in which six subjects were examined with the same techniques, confirmed and supported the present results.

Figure 7 summarizes the relationship between average IEMG and the average force for the various jumping conditions of the study (V). The slope of this IEMG/force ratio, when examined in the eccentric phase of DJ and CMJ, suggests that a lesser amount of EMG activity is needed per unit of force than in SJ. This agrees well with observations on constant speed or force movements, that fewer motor units are activated during eccentric than during concentric contraction to produce the same force (e.g. Abbott et al. 1952, Bigland and Lippold 1954, Asmussen 1971, Komi 1973). These findings can be explained by a recent study made by Flitney and Hirst (1978), in which it was pointed out that during the stretching phase, part of the tension is taken up by the elastic elements being arranged in series with the sarcomeres. In addition, Flitney and Hirst (1975), utilizing the model proposed of Huxley and Simmons (1971), have suggested that a forcibly stretched muscle can modify the cross-bridges by rotating the myosin heads backwards against their natural tendency to a position of higher potential energy. In fact, this means storage of mechanical energy in the internal structure of the muscle. This can be recovered during the following concentric phase if the muscles are allowed to shorten immediately after the stretching (Cavagna et al. 1965). The effect of the recovery of elastic mechanical energy was confirmed in the present study, and can be deduced from the right side of Figure 7. It is evident that in the positive work phase of both CMJ and DJ, a lesser amount of EMG activity is needed per unit of force when compared to SJ conditions. Furthermore it is worth noting that the potentiation effect in the case of DJ was more of elastic nature than was true for CMJ. The explanation for this must be sought, as already suggested, in the high myoelectrical activity which characterized the eccentric work of

DJ. This increased mechanical activity modifies the viscoelastic properties of the muscle with added stiffness, and therefore the possibility of storing elastic energy within the muscle increases.

In addition, the increased stiffness makes the transition from the eccentric to the concentric phase take place more quickly. This hypothesis is suggested by the negative correlation ($p < .001$) between the force developed at end of the stretch (F_i) and the coupling time; this is shown in Table 2. Furthermore, the present findings support the hypothesis of Houk (1972) and Nichols and Houk (1976), who suggested that the function of the stretch reflex is to compensate for variation of muscle properties, and that one by-product of such regulation might be stiffness.

Besides also CNS operates to regulate muscle contraction. It should be made clear that myotatic reflex, especially in ballistic movement, may operate with great efficiency to match the viscoelastic properties of the muscle so that movement can be accomplished in an economical way.

In counter-movement jump the average eccentric force, as it was measured in the present study, did not behave in the same way as in the drop jump conditions. In fact, this force decreased with increase in stretching speed. Simultaneously, the IEMG activity of the muscles investigated (vastus lateralis and medialis) stayed at high level.

The stretching speed increased because the loads were decreased, and it is likely that the effects of decreasing extra loads might shift the performance from a "smooth ramp motion" to a "ballistic type". However, despite the low eccentric force, the potentiation effect in the subsequent positive work phase was substantial, and in agreement with Cavagna's (1977) suggestions. Because IEMG activity was high in the eccentric phase, one would have expected higher force values as well. However, the present data is not sufficient to explain the possible reason for the observed high level EMG activity and simultaneously recorded low average force value during the eccentric phase of CMJ. Whether the observed phenomenon can be related to possible differences in motor units recruitment patterns between the different kind of CMJ (with and without loads) cannot be answered as well.

Table 3 shows that the efficiency of positive work in stretch-shortening cycle performance was affected by movement amplitude. This observation is in good agreement with the findings of Thys et al. (1972, 1975) and Asmussen and Bonde-Petersen (1974b). They suggested that the better efficiency observed in small amplitude exercises is due to the recoil of elastic elements, which affect mainly the first part of the positive phase. However, it should be remembered that even in large amplitude jump, the observed mechanical efficiency was greater than that calculated for the jumping condition without rebound; the figures being 26-30 % and 19.6 %, respectively. On the other hand, it should be pointed out that the increased efficiency in rebound jumps is, as suggested by Cavagna (1977), also due to the fact that previous stretching decreases the time in which positive work is done during the subsequent shortening. It follows that, to perform a given amount of work, the muscle remains active for a shorter time; and consequently less chemical energy is set free. In Figure 8 it is demonstrated that IEMG activity during either negative or positive phase of rebound jump was always lower than that observed in squatting jump. This means that motor unit activation of leg extensor muscles in rebound jumps was working at a submaximal level, regardless of the tension developed. In spite of this, in rebound jumps motor unit activation was much lower than observed in the eccentric work phase of DJ and CMJ, where it in some cases was potentiated over the "maximal". It seems that storage and utilization of elastic energy operates with the same mechanism in all conditions. Therefore, if on one hand the absolute amount of elastic energy stored is smaller during the stretching of a muscle in submaximal contraction, and on the other hand, the absolute amount of chemical energy utilized by the muscle is also decreased in submaximal contraction (Cavagna 1977), then it is likely that the ratio between the chemical energy used and the elastic energy reutilized may not change much with the number of motor units activated (Cavagna 1977). Thus, the present findings support Cavagna's (1977) suggestions that an active stretch-shortening mechanism can indeed operate for each active fiber at all levels of motor units recruitment. It is obvious that the total amount of mechanical energy stored can be greater, the more extensive the activation of motor units, and consequently the increase in muscle stiffness during eccentric work. This can explain why high efficiency was associated with the rebound jump conditions, in which high muscular stiffness was observed in eccentric work, as well as shorter coupling time and higher stretching speed. Perhaps the most relevant finding might be that low efficiency was associated with greater IEMG activity during concentric work. This suggests that a large amount of the positive work was performed by greater recruitment of contractile machinery of the muscle, with a consequent utilization of a larger amount of chemical energy. In addition, the low IEMG activity noted in the concentric work phase of small amplitude jumps, as well as that observed in the concentric work phase of DJ (Figures 4 and 5) makes these conditions the most favorable under which to benefit from the recoil of elastic structure. The exact mechanism which operates to decrease myoelectrical activity during concentric work in those conditions is not yet clear. However, in both rebound jumps and under DJ conditions, high acceleration is developed at the beginning of concentric work. In this connection, Angel (1974) suggested that the sudden unloading of muscle spindle might decrease the proprioceptive feedback. However, this suggestion could be questioned, because probably the time is too short to enable this mechanism to operate properly. On the other hand, this explanation is by no means fanciful, and therefore should be kept also in mind.

Inhibition from GTO might be an other mechanism, because of the high tension developed at the end of the eccentric phase (Angel 1974). Perhaps this seems more likely to be true, at least on the basis of the present results for DJ conditions. However, the possibility remains that the effect derives from a combined effect of both mechanisms, or from a deactivation of the voluntary drive of motor units.

To estimate the proportion of extra work done due to the reutilization of elastic energy during the positive work in rebound jumps, the formular of Alexander and Vernon (1975) can be used:

$$E_{pos} \times 0.2 = W_{pos} - W_{el} \longrightarrow W_{el} = W_{pos} - 0.197 \times E_{pos}$$

where W_{pos} is the positive work, E_{pos} is the energetic cost of positive work, W_{el} is the work due to the re-use of elastic energy and 0.197 is the efficiency of the contractile machinery of the muscles measured in the series V of jumps.

The contribution of W_{el} to the total positive work in the average jump amounted to about 50 % in small amplitude jumps and 30 % in large amplitude exercise (Figure 10). However, it can be seen that in absolute value, W_{el} was higher in large amplitude jumps. It is interesting to note that, if the elastic energy were stored only in the tendons, higher W_{el} should have been observed in small amplitude jumps. This exercise favours the storage of a greater amount of potential energy in connective tissue, because of the high average force ($\bar{F}$) and instantaneous force developed at end of the stretch (F_i) (Table 3). Thus our results support the findings of Huxley and Simmons (1971) and Cavagna and Citterio (1974) that elastic energy is mainly stored in the contractile machinery of the muscles.

It should be remembered that Cavagna and Citterio (1974) have suggested that modification of muscle elastic elements, induced by previous stretching, is a transient phenomenon and tends to disappear shortly after stretch. This transient character has been assumed to be estimated by the coupling time (Table 2). In order to utilize the stored elastic energy, the coupling time should be shorter than the cross-bridges' life time. Curtin et al. (1974) estimated the mean cycle times of cross-bridges during work and isometric contraction to 120 ms and 340 ms, respectively. Shorter cross-bridge life time has been suggested by

Stienen et al. (1978); they suggested that the average duration of cross-bridge attachment is about 15 ms. Therefore, in view of these findings, it is somewhat surprising to note how in large amplitude jumps, high W_{el} was observed in some subjects in spite of a long coupling time (≈ 150 ms).

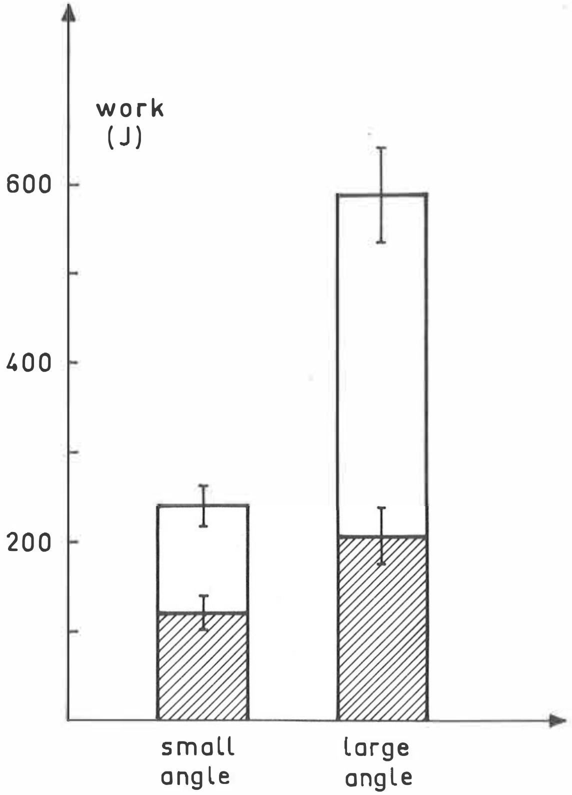

Figure 10. Positive mechanical work calculated for the average jump of small and large knee angular displacement rebound conditions, performed without extra load (mean ± SD). The hatched area denotes the estimated work done by the restitution of stored elastic energy (mean ± SD).

To try to explain this phenomenon it should be remembered that the minimum duration of coupling time to allow the re-use of elastic energy might be connected to the types of the whole fibers activated. Human skeletal muscles are composed of fast and slow fiber types, and they differ e.g. in respect of their twitch mechanograms (Eberstain and Goodgod 1968, Lännergren 1974) so that fast twitch fibers (FT) can produce their force faster and relax quicker than slow twitch fibers (ST). In the present study, large amplitude jumps were characterized by low knee angular velocity as well as low average force in both eccentric and concentric work (Table 3). In this connection it should be mentioned that it has been suggested that in slow, not powerful contractions, it is mainly ST fibers that are recruited (e.g. Henneman et al. 1965, Gydikov and Kosarov 1974, Tanji and Kato 1973). Therefore it is possible that in large amplitude jumps, the contribution of ST fibers to the performance could be predominant. This suggestion is not in disagreement with the study of Komi and Bosco (1978b) where the effect of elasticity, and its association with muscle fiber composition, was influenced by the mechanical movement pattern during the vertical jump. Now considering that it has been demonstrated that ST fibers have a long cross-bridge engagement time (e.g. Goldspink et al. 1970, Goldspink 1978), it can be suggested that in spite of the long coupling time, store and utilization of elastic energy have occured in ST fibers because of their slow dynamic characteristics. On the other hand, probably the coupling time was too long to allow the stored elastic energy in FT fibers to be fully utilized, taking into consideration that the cross-bridge life of FT is very short (Barany 1967, Goldspink et al. 1970, Goldspink 1978). The longer life time of the cross-bridges in ST muscles have been explained also by the slower initial decay of the active state (Wells 1965). This would then favour the slow fibers to maintain longer the potential elastic energy, when the muscle is stretched during the eccentric work. Figure 11 attempts to explain this mechanism schematically, when ST and FT fibers are examined in different combinations of con-

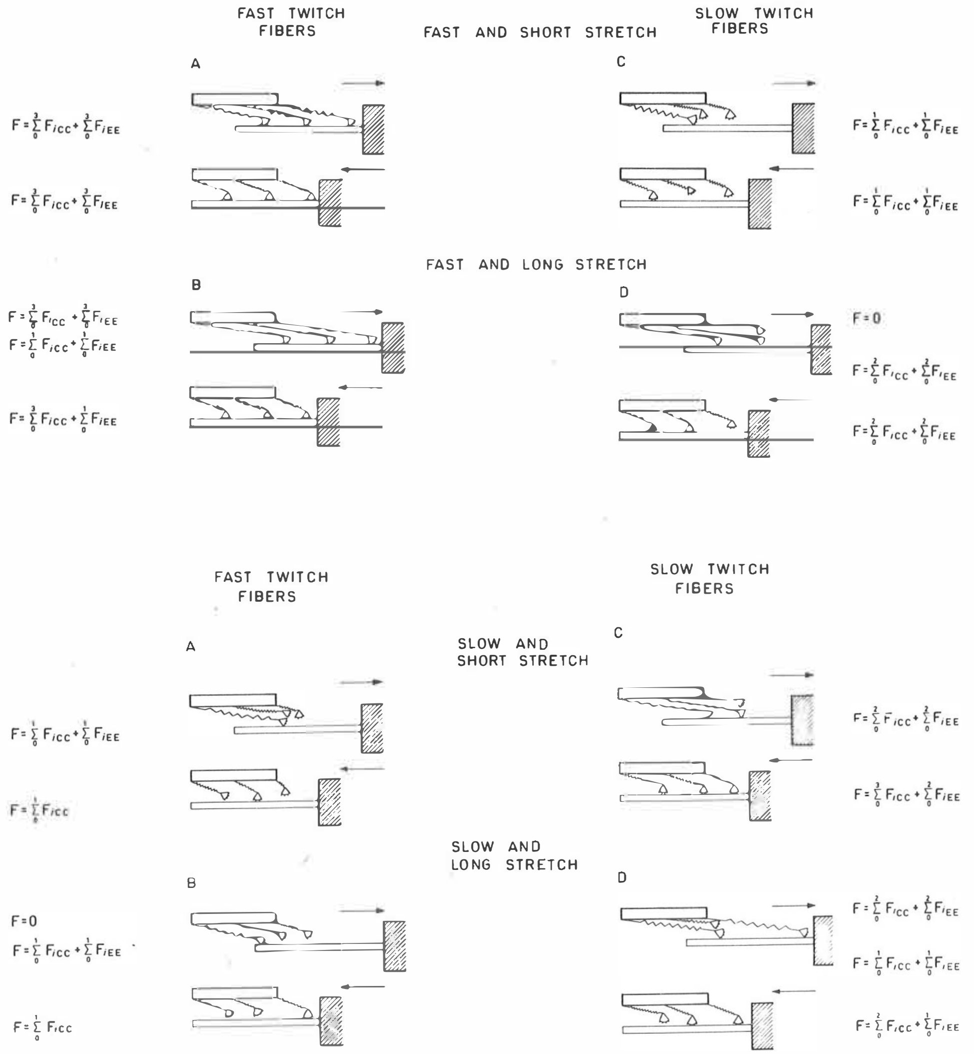

Figure 11. A schematic model to suggest the attachment and detachment of actomyosin cross-bridges cycle in fast twitch (left) and slow twitch (right) fibers, working at different speeds and with different lengths of stretch. The calculations treat the cross-bridges working in parallel with each other. In conditions B and D, two equations are shown for the stretching phase. The upper equation refers to the cross-bridge status at the beginning of the stretch, and the lower to that at the end. This model, too, is based on the hypothesis of Huxley and Simmons (1971) and Cavagna and Citterio (1974).

traction. In this connection, it is relevant to note that Asmussen et al. (1976) found that the potentiation effect of the stretch-shortening cycle, during vertical jump performance, was enhanced when the temperature of human leg extensor muscles was lowered to about 32°C. This result was attributed mainly to the fact that at low temperatures, the cross-bridge life is lengthened. Therefore, this allows a great amount of elastic energy stored during the stretching phase, to be reutilized during concentric work.

In the present study, in contrast to the large jumps, small amplitude jumps were characterized by higher knee angular velocity as well as greater force in both eccentric and concentric phases (Table 3). Therefore, it is reasonable to assume that different patterns of fiber recruitment might have occured from those characterizing large amplitude jumps; and FT fibers could have played a primary role in contributing to the performance (Gillespie et al. 1974). In this connection, Bosco and Komi (1979) have shown a positive relationship between percentage of FT fibers and maximal vertical jump performance. Nevertheless, as we discuss above, even though the life time of cross-bridges in FT is short, a great amount of W_{el} was observed in small rebound jumps. This finding, obviously, can be explained by the fact that the fast stretch-shortening cycle is characterized by a short coupling time, which allows the stored elastic energy to be utilized during positive work.

In conclusion, assuming that W_{el} is related to both the square of the stretching length and to muscle stiffness, it is interesting to note, how the viscoelastic properties of the skeletal muscle can benefit from stretch-shortening. Thus if, on one hand, in small amplitude jumps the muscle stiffness is higher, the change in muscle length is small. On the other hand, if the stretching length is increased (large amplitude jumps) the stiffness decreases. Therefore, the present findings suggest that the mechanical behaviour of human skeletal muscle has evolved during phylogeny to meet the requirements for natural movement and one of these seems to be the ability to benefit from the stretch-shortening cycle which is generally determined by environmental conditions (such as gravitational pull).

TIIVISTELMÄ

Aktiivisena olevan poikkijuovaisen lihaksen venyttäminen varastoi siihen elastista energiaa, joka voidaan hyödyntää välittömästi seuraavassa konsentrisessa supistuksessa. Eristetyllä lihasnäytteellä tehdyissä tutkimuksissa venytyksen aikaansaama suorituksen paraneminen aiheutuu pelkästään elastisen energian hyödyntämisestä, kun taas ihmisellä tehdyissä kokeissa lihaksen aktiviteetin reflektorinen ohjaus saattaa osaltaan lisätä suoritustehoa. Tämän problematiikan selventämiseksi toteutettiin viisiosainen tutkimussarja. Ensimmäiseksi tutkittiin jalkojen ojentajalihasten käyttäytyminen venytys-supistussyklin aikana suhteutettuna ikään ja sukupuoleen (I), toiseksi selvitettiin saman lihasryhmän voima/nopeus- ja teho/nopeus -riippuvuudet esivenytyksen kanssa ja ilman sitä tehdyissä vertikaalihypyissä (II). Kolmannessa vaiheessa tutkittiin erilaisten mekaanisten parametrien väliset yhteydet venytys-supistussyklissä (III). Edelleen tutkittiin elastisen energian hyödyntämisen ja lihaksen EMG-aktiviteetin yhtäaikainen vaikutus voima/nopeus- ja teho/nopeus -riippuvuuksiin (IV), ja lopuksi selvitettiin esivenytyksen vaikutus lihastyön taloudellisuuteen (V).

Tutkimuksiin osallistui yhteensä 113 mies- ja 113 naispuolista koehenkilöä. Tavanomaisin tilastollisin menetelmin laskettiin keskiarvot, keskihajonnat, keskihajonnan keskivirheet sekä lineaariset korrelaatiokertoimet. Käytettyjen mittausmenetelmien tarkkuus arvioitiin mittavirheiden avulla. Vertikaalihypyt suoritettiin voimalevyanturilta seuraavasti: staattinen hyppy (SJ) ilman esikevennystä, esikevennyshyppy (CMJ) sekä pudotushypyt (DJ) eri pudotuskorkeuksilta (20-100 cm). Lisäksi SJ- ja CMJ-hyppyjä suoritettiin lisäpainoilla, 15-220 % kehon painosta (tutkimukset I-IV). Viidennessä osatutkimuksessa tehtyjen yhden minuutin hyppelysarjojen aikaisesta hengitysilmasta laskettiin hapenkulutus. Polvikulman muutokset rekisteröitiin sähköisellä goniometrillä. Lisäksi tutkimuksissa IV ja V taltioitiin lihasten EMG-aktiviteetti jalkojen ojentajalihaksista.

Odotusten mukaisesti saavuttivat miehet naisia parempia arvoja vertikaalihypyistä mitatuissa mekaanisissa muuttujissa, esim. keskiarvovoimassa, keskiarvotehossa, nettoimpulssissa ja kehon painopisteen nousukorkeudessa. Erot kuitenkin pienentyivät, kun tulokset suhteutettiin kehon painoon. Lisäksi lapsilla ei havaittu eroja eri sukupuolten välillä. Suorituskyvyn huippu saavutettiin sekä miehillä että naisilla 20-30 ikävuosien välillä, jonka jälkeen suoritusteho heikkeni lineaarisesti. Samalla tavoin iän myötä heikkeni kyky esivenytyksen hyödyntämiseen mekaanisen työn lisäämisen suhteen. Mekaanisen työmäärän lisääntyminen lihassupistuksessa esivenytyksen seurauksena voitiin todistaa myös vertikaalihypyistä laskettujen voima/nopeus- ja teho/nopeus -käyrien avulla. Lihaksen esivenytys (CMJ- ja DJ-hypyt) siirsi kumpaakin käyrää oikealle, verrattuna staattisista hypyistä laskettuihin käyriin. Absoluuttisina voima- ja tehoarvoina parannus oli 40-500 %. Esivenytyksen aiheuttama suorituskyvyn paraneminen on oletettu johtuvan elastisen energian hyödyntämisen ohella lihaksiston EMG-aktiviteetin reflektorisesta lisääntymisestä. EMG-aktiivisuudet esikevennyshyppyjen eksentrisissä ja konsentrisissa vaiheissa eivät kuitenkaan eronneet staattisten hyppyjen aktiivisuuksista. Sen sijaan pudotushyppyjen eksentrisissä vaiheissa havaittiin suuri EMG-aktiviteetti, joka tosin heikkeni suuremmilta pudotuskorkeuksilta pudottauduttaessa.

Esivenytyksen vaikutus suoritukseen havainnollistettiin myös hyötysuhteen avulla. Kimmoisissa hyppelyissä, joissa siis esivenytystä käytettiin, hyötysuhde oli 38.7 % (pieni polvikulman muutos, pohjehyppely) tai 30.1 % (suuri polvikulman muutos, kyykkyhyppely). Ilman esivenytystä tehdyissä hyppelyissä hyötysuhde oli keskimäärin vain 19.7 %.

Miesten saavuttamat paremmat tulokset oletettiin johtuvan heidän suuremmasta lihasmassastaan naisiin verrattuna. Vertikaalihyppyominaisuuksien heikkeneminen iän myötä saattaa aiheutua maksimaalisissa supistuksissa tarvittavien nopeiden lihassolujen prosentuaalisen osuuden pienenemisestä, mikä tosin ei sulje pois mahdollisuutta vanhempien ihmisten koordinaatiokyvyn puutteesta. Esivenytyksen aiheuttaman suorituskyvyn paranemisen sekä voima/nopeus- ja teho/nopeus -käyrien oikealle siirtymisen syiksi esikevennys- ja pudotushypyissä voidaan olettaa elastisen energian hyödyntäminen sekä lihaksiston reflektorinen aktivoituminen. Näistä EMG-aktiviteetin potentoituminen oli suurempaa pudotushypyissä, joissa kuitenkin tietyn pudotuskorkeuden jälkeen mitattu EMG-aktiviteetti heikkeni. Tällöin Golgin jänne-elimen inhibitorinen refleksi luultavasti ylittää esivenytyksen fasilitatoriset vaikutukset.

Kuten jo edellä mainittiin, oli kimmoisissa hyppelysarjoissa hyötysuhde parempi kuin ilman esivenytystä suoritetuissa hyppelyissä (30-38 % vs 20 %). Tämä voidaan katsoa johtuvan sekä elastisen energian hyödyntämisestä että konsentrisen vaiheen alhaisesta EMG-aktiviteetista kimmohyppelyissä. Suuri määrä positiivista työtä voidaan tehdä ilman supistuvan koneiston aineenvaihduntaa. Elastisen energian säilymisen ehdoksi on esitetty lyhyttä siirtymäaikaa eksentrisen ja konsentrisen supistusvaiheen välillä. Sen vuoksi olikin yllättävää havaita esivenytyksen suuri hyödyntäminen kyykkyhyppelysarjoissa, joissa polvikulman muutos oli suuri ja kyseinen siirtymäaika pitkä. Tämä voidaan kuitenkin selittää olettamalla, että työ kyykkyhyppelyissä suoritettiin pääasiallisesti hitailla lihassoluilla, joiden aktiivinen supistus on pitkäkestoinen.

Jos oletus hitaiden lihassolujen käytöstä suuriamplitudisissa hyppelyissä pitää paikkansa, tuo esiteltävä tutkimus esiin mahdollisuuden hitaiden ja nopeiden lihassolujen eroavasta käyttäytymisestä venytys-supistussykleissä elastisen energian hyödyntämisen suhteen. Tehdyn dynaamisen työn luonteella on tällöin ratkaiseva merkitys. Loppuyhteenvetona voidaan esittää ballistisen liikkeen tehokkuuden edellytykseksi eksentrisen vaiheen suuri EMG-aktiviteetti. Korkea EMG:n määrä aiheuttaa välisiltojen suuren aktivoitumisen, joka puolestaan parantaa mahdollisuutta elastisen energian hyödyntämiselle positiivisen työvaiheen aikana.

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